

# Host Species and Host Plant Effects on Preference and Performance of *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae)

A. EBEN,<sup>1, 2</sup> B. BENREY,<sup>1</sup> J. SIVINSKI,<sup>3</sup> AND M. ALUJA<sup>4</sup>

Environ. Entomol. 29(1): 87-94 (2000)

**ABSTRACT** Naive female *Diachasmimorpha longicaudata* (Ashmead), a solitary endoparasitoid of tephritid fruit flies, exhibited positive responses toward volatiles of host fruits in olfactometer and wind tunnel bioassays. Although no significant preference for one of the test fruits, mango, *Mangifera indica* L., or grapefruit, *Citrus paradisi* Macfaden, was observed, the number of flights in the wind tunnel was higher in the presence of mangos. In the olfactometer trials, parasitoids preferred fly infested over noninfested grapefruits, and infested over noninfested mangos. Reproductive performance bioassays were conducted using *Anastrepha ludens* (Loew) larvae (Diptera: Tephritidae) reared in grapefruit, orange, mango, or artificial diet, and *Anastrepha obliqua* (Macquart) larvae reared in mango as parasitoid hosts. Parasitoid performance was compared for 2 *Anastrepha* species and 3 fruit species. Significant effects of fruit fly species and of the diet of fruit fly larvae on longevity, size, and progeny production of *D. longicaudata* were observed. *Anastrepha ludens* reared in grapefruit was the best host in terms of offspring longevity, size, and number of female progeny, but parasitoids that developed in *A. ludens* reared in mango had higher overall fecundity. *Anastrepha ludens* reared in mango was a better host than *A. obliqua* in the same fruit. No correlation between parasitoid size and demographic parameters was found. The results of this laboratory study showed that host preference and offspring performance are partially related.

**KEY WORDS** Tephritidae, *Anastrepha* spp., Braconidae, *Diachasmimorpha longicaudata*, chemical ecology, tritrophic effects

A FOCUS OF parasitoid behavioral ecology during the last 2 decades has been to understand how parasitoids detect their hosts. Chemical and visual cues of herbivorous hosts, their food plants, and habitats have been found to play a major role in the searching behavior of parasitic wasps (Vet and Dicke 1992, Messing et al. 1996, Ngi-Song et al. 1996). In several cases it was observed that damaged plants are a source of volatiles that attract parasitoids to their hosts (Nadel and van Alphen 1987, Turlings et al. 1989). This was interpreted as an induction of plant defenses after feeding damage by herbivores (Dicke and Sabelis 1988, Mattiacci et al. 1994). Tritrophic level studies have further investigated the effects of host quality and of the chemical composition of food plants on parasitoid development and survival (Barbosa et al. 1986).

The relationship between oviposition preference and performance of herbivore offspring is the most thoroughly examined question in the study of insect/plant interactions (Singer et al. 1988, Thompson 1988). However, relatively few studies have investigated how

host plant preferences influence the searching behavior and performance of parasitic wasps (Vet et al. 1993, Hedlund et al. 1996). The effect of the host plant of a polyphagous herbivore on life history parameters and fitness of its parasitoid is still less investigated (Benrey et al. 1998).

The objective of this study was to determine the effects of host fruit volatiles on parasitoid host-searching behavior. Further, we measured the consequences of host diet on parasitoid offspring by comparing parasitoid performance in 2 fly species reared in fruits from 2 host plant families. Our hypothesis was that parasitoids prefer host plants and host species that resulted in the best performance (size, sex ratio, fecundity, and longevity) for their offspring. *Diachasmimorpha longicaudata* (Ashmead) is a solitary late-instar larval-pupal endoparasitoid of fruit flies. Females detect their hosts through vibrations and sounds produced by fly larvae while they feed within fruits (Lawrence 1981). *Diachasmimorpha longicaudata* is currently mass released in several countries for biological control of tephritid flies (Wharton et al. 1981, Sivinski et al. 1996). It has been observed that this parasitoid responds to fruit size (Sivinski 1991), color (Vargas et al. 1991), and volatiles (Leyva et al. 1991), but few detailed behavioral studies on tritrophic interactions have been published on *D. longicaudata* (Rodríguez 1991). An understanding of the fitness consequences of herbivore host plants and herbivore species on natural enemies such as parasitoids is crucial for bio-

<sup>1</sup> Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, México D.F. C.P. 04510, Mexico.

<sup>2</sup> Current address: Instituto de Ecología, A.C., Apartado Postal 63, 91000 Xalapa, Veracruz, Mexico, e-mail: astrid@ecologia.edu.mx

<sup>3</sup> Center for Medical, Agricultural and Veterinary Entomology, USDA-ARS, Gainesville, FL 32608.

<sup>4</sup> Instituto de Ecología, A.C., Apartado Postal 63, 91000 Xalapa, Veracruz, Mexico.

logical control programs and for interpreting parasitoid population dynamics under field conditions.

### Materials and Methods

**Parasitoid Rearing.** Parasitoid colonies were maintained at  $26 \pm 1^\circ\text{C}$ , 70% RH, 400 lux, and a photoperiod of 12:12 (L:D) h at the Instituto de Ecología, A.C. in Xalapa, Veracruz, Mexico. Third instars from a laboratory colony of *Anastrepha ludens* (Loew) reared on artificial diet (M. Aluja and I. Jácome, unpublished data) were used as hosts.

**Test Fruits.** Fruits used in the experiments were exposed to cohorts of *A. ludens* and *A. obliqua* (Macquart) fruit flies to obtain material infested by fly larvae. These cohorts were obtained from field-infested grapefruits, *Citrus paradisi* Macfaden, and mangos, *Mangifera indica* L. From these fruits, we collected pupae, and later used the adult flies to infest the respective fruits (i.e., grapefruit or mango) in the laboratory. Infested fruits were kept in an open greenhouse under ambient temperature until *Anastrepha* larvae reached the 3rd instar. Uninfested fruits purchased at local markets were used as controls in the experiments. Oranges, *Citrus aurantium* L., used for the performance bioassays were naturally infested fruits collected from orchards in various locations in the state of Veracruz.

**Host Location Experiments.** To determine the preference of *D. longicaudata* females for infested and uninfested fruit of various species we conducted a series of olfactometer and wind tunnel trials.

**Olfactometer Trials.** To determine the preference of parasitoid females for volatiles of infested and uninfested fruits, grapefruits and mangos were offered in choice and no choice tests to individual parasitoids using a Y-tube glass olfactometer (Sabelis and Van de Baan 1983, Ngi-Song et al. 1996). Tests were conducted in the laboratory at  $26 \pm 1^\circ\text{C}$ ,  $50 \pm 5\%$  RH, and 600 lux. Light was provided by a light bulb (60 cm, 500 V) hung above the olfactometer. All tests were done between 0900 and 1400 hours. A test fruit in a sealed plastic bag or an empty plastic bag (blank) was connected to each arm of the olfactometer. Compressed air (100 kPa/s) was blown through a charcoal filter and humidified before passing through Teflon tubes into the bags with fruits and then through the olfactometer. Parasitoids used for the experiments were allowed at least 1 h for acclimatization to ambient conditions before testing. Individual female parasitoids (5–9 d old) were captured with a glass vial from the laboratory colonies and the vial was placed horizontally with the opening upwind into the olfactometer. After a female left the vial it was observed for 5 min. If a female did not reach the center of the olfactometer within 5 min, its reaction was registered as no choice. Observation time was stopped when the parasitoid entered 1 arm of the olfactometer and reached the bag with the test fruit or when it crossed an imaginary line that divided the arm into 2 equal halves and stayed at least 30 s beyond the line. For each odor combination, 100 females were observed in 10 blocks

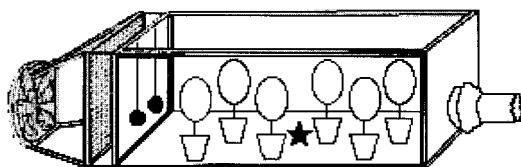


Fig. 1. Wind tunnel used in the host location experiment. Fruits were hung in pairs from the ceiling at the upwind end. Six fruit trees in pots were placed in the tunnel. Asterisk indicates the release point of the female parasitoids in the center of the tunnel.

of 10 females per day. Each insect was tested only once. Plastic bags were switched between arms after each female to avoid position effects. After each trial the olfactometer was rinsed with ethanol to remove all odors. Responses to all 5 combinations were observed per day in a random order and repeated 10 times. Each day was treated as a block in a randomized complete block design. Results from the dual choice tests were compared using the chi-square test for goodness-of-fit ( $P = 0.05$ ) (Sokal and Rohlf 1995).

**Wind Tunnel Trials.** To study the flight behavior of parasitoids when presented with infested and uninfested fruits, female parasitoids were observed in a wind tunnel. The tunnel was constructed from transparent Plexiglas (150 by 50 by 50 cm) and covered on all sides with white cloth. Indirect light of 600 lux inside the tunnel was provided with 3 fluorescent bulbs each at top and bottom (each 1.1 m long). Additionally, white paper with orange and black stripes was placed under the bottom of the tunnel to provide visual orientation cues to the parasitoids (Elzen et al. 1986). Air was blown into the tunnel by a fan through a charcoal filter and pulled through the tunnel by a tube that connected the downwind end of the tunnel with the exhaust system of the building. Wind speed at the release point of the parasitoids was between 0.1 and 0.2 m/s. To mimic natural turbulence, 6 orange or mango trees in pots were placed together with the respective fruits in the tunnel (based on Aluja et al. 1993). Artificial trees were used for the grapefruit/mango combination. Two fruits were placed in various combinations on wire mesh trays and hung at medium height in upwind direction from the ceiling of the tunnel (Fig. 1). As for the olfactometer trials, parasitoids used for the experiments were allowed at least 1 h for acclimatization to ambient conditions before testing. Ten female parasitoids (5–9 d old) were captured with a glass vial from a laboratory colony and released in the center of the tunnel (Fig. 1). A stopwatch was started when the 1st parasitoid left the vial and parasitoids were observed for 15 min. All flights, hoverings, and landings performed were recorded. Only the 1st movement of each of these behaviors of each female counted as a response. Day to day variation in the response of parasitoids to volatiles has been reported for several species (Steinberg et al. 1992) and could be clearly observed for *D. longicaudata* (A.E., unpublished data). Increased barometric pressure resulted in higher activity and stronger re-

**Table 1.** Species combinations used in bioassays to test for the effects of fruit species and fly species on parasitoid performance

Third trophic level	<i>Diachasmimorpha longicaudata</i> (Ashmead)	
Second trophic level	<i>Anastrepha ludens</i> (Loew)	<i>Anastrepha obliqua</i> (Macquart)
	<i>Mangifera indica</i> L.	<i>Mangifera indica</i> L.
First trophic level	<i>Citrus aurantium</i> L.	
	<i>Citrus paradisi</i> Macfaden	
	Artificial diet	

sponses of the females. To control for this effect, days were treated as blocks and experiments were only conducted during days with clear skies and sunshine. For each fruit combination, 120 females were observed in groups of 10 females per day. The citrus and mango trees without the respective fruits served as control. For the controls, 60 females were observed in groups of 10 individuals. Each insect was used only once. Responses to all 9 combinations were observed per day in a random order and repeated 12 times (12 blocks). Between each group of insects, the position of fruits was switched to avoid positional effects. Wind tunnel experiments were conducted at the Instituto de Ecología, UNAM, Mexico, DF, at  $25 \pm 1^\circ\text{C}$ ,  $45 \pm 5\%$  RH. All tests were done between 0900 and 1400 hours. Results from wind tunnel trials were compared using the chi-square test for goodness-of-fit. In all cases,  $P = 0.05$  was used to determine significant differences (Sokal and Rohlf 1995).

**Performance Bioassays.** To examine the effects of host fruit and fruit fly species on the performance of *D. longicaudata* females, parasitoids developed in *Anastrepha* larvae that had been reared in different fruits and artificial diet were used (Table 1). Third instar larvae of *A. ludens* were collected from grapefruit, oranges and mango, infested in the field or by 1st generation laboratory flies. Third-instar *A. obliqua* larvae were collected from mangos infested from 1st generation laboratory colonies. Lawrence et al. (1978) reported a host:parasitoid density of 30:1 as optimal for 24-h oviposition experiments. Based on this ratio we exposed 100 larvae per fruit and fly species to 10 female parasitoids during 8 h. Larvae were allowed to pupate, and pupae were maintained in moist, sterile vermiculite until emergence of parasitoids and flies. Numbers of flies and female and male parasitoids were recorded. This was repeated until at least 30 females were obtained in the  $F_1$  generation of parasitoids for each host fruit/fly species combination. Female and male parasitoids were kept together for 5–7 d to allow time for mating. The female:male ratio ranged from 1:1 to 3.6:1.

To determine life history parameters of parasitoids that emerged from each fruit/fly species combination, 30 mated females (5–7 d old) from each fruit/fly species combination were placed individually in oviposition containers (500-ml plastic containers) with a honey-water diet. Ten uniformly sized, 3rd-instar *A. ludens* larvae reared on artificial diet served as oviposition hosts for each parasitoid. Each female was allowed to oviposit for 8 h daily during its entire lifetime. Larvae were removed after these 8 h. Pupae were

maintained until emergence of parasitoids and flies. For each female we recorded longevity, body size, total number of progeny, and sex of progeny. Hind tibia length was used to express female body size. It was measured using a microscope equipped with an ocular micrometer (STEM SV 8, Zeiss) (Jenna, Germany). The effect of fruit and fly species on longevity and size of parasitoids was analyzed using an analysis of variance (ANOVA). Means were separated with a least significant difference (LSD) test ( $P < 0.05$ ) (Statgraphics 1991). The same ANOVA procedure was used to examine effects of host diet on parasitoid fecundity. Before analysis, data for proportions of parasitized fly larvae were arcsine transformed to meet assumptions of normality. Means were separated with an LSD comparison. A linear regression was used to describe the relationship between body size and fecundity, longevity and offspring sex ratio (Sigmastat 1992). Laboratory experiments were conducted at the Instituto de Ecología, A.C. in Xalapa, Veracruz.

## Results

**Effect of Host Fruit on Parasitoid Host Location. Olfactometer Experiment.** Female parasitoids showed a significant positive reaction ( $P < 0.05$ ) toward the odor of infested mangos ( $\chi^2 = 389.76$ ,  $df = 1$ ) and grapefruits ( $\chi^2 = 97.41$ ,  $df = 1$ ) when the fruits were offered under choice conditions (infested versus uninfested fruit). Infested mangos ( $\chi^2 = 4.06$ ,  $df = 1$ ), and infested grapefruits ( $\chi^2 = 21.81$ ,  $df = 1$ ) were significantly preferred over the respective noninfested fruits. No preference for infested mangos or grapefruits could be observed when the volatiles of both fruits were presented simultaneously (Fig. 2).

**Wind Tunnel Experiment.** Only 10 out of 840 females released in the tunnel actually flew and landed on a fruit. In 9 cases these fruits were mangos. When comparing the proportions of females that flew upwind toward the odor source and proportions that flew downwind away from the odor source, it was observed that significantly ( $P < 0.05$ ) higher numbers of parasitoids flew upwind when an infested mango was offered together with an infested grapefruit ( $\chi^2 = 10.6$ ,  $df = 1$ ) or with an uninfested mango ( $\chi^2 = 14.67$ ,  $df = 1$ ), or when 2 uninfested mangos were present ( $\chi^2 = 6.31$ ,  $df = 1$ ). In general, the proportion of parasitoids that flew in the tunnel was higher when mangos were present in any of the combinations compared with grapefruit. In the case of the control treatment (trees but no fruit odor source present), significantly higher numbers of parasitoids flew downwind than upwind (mango,  $\chi^2 = 23.95$ ,  $df = 1$ ; grapefruit,  $\chi^2 = 10.25$ ,  $df = 1$ ) (Fig. 3).

**Effect of Host Fruit and Fly Species on the Performance of Parasitoids. Size and Longevity of Parasitoids.** Female parasitoids that emerged from *A. ludens* reared in oranges (hind tibia length:  $1.85 \pm 0.03$  mm [mean  $\pm$  SE]) and grapefruits (parasitoid parent generation [Fp] generation from a wild cohort obtained from fly infested fruits parasitized under natural field conditions) ( $1.85 \pm 0.02$  mm) were significantly larger than

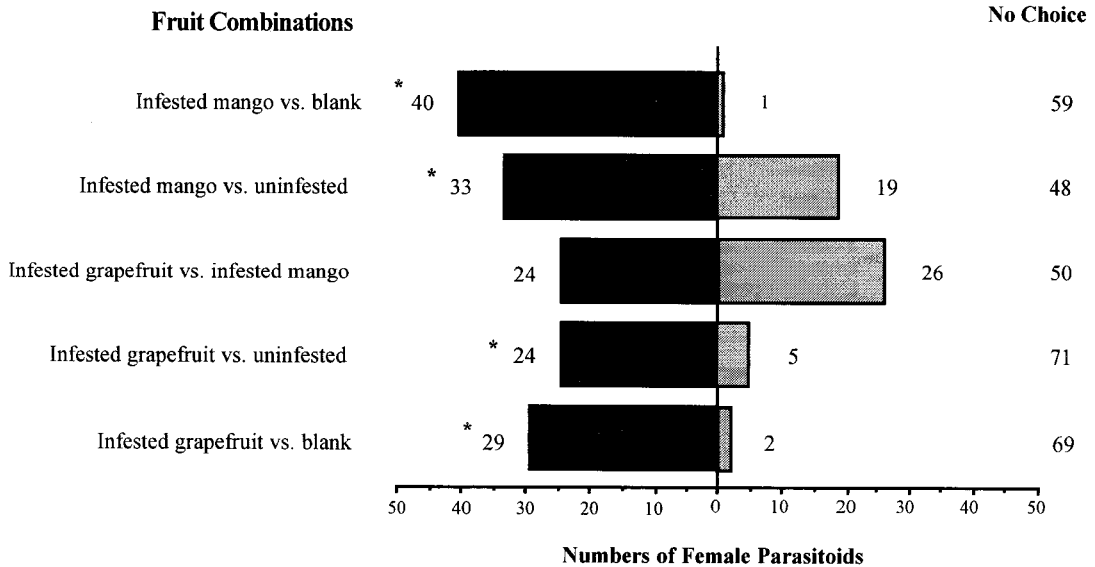


Fig. 2. Combinations of fruits offered to female parasitoids in choice tests with an olfactometer ( $n = 100$ ). Asterisks indicate significant differences ( $P = 0.05$ ) within the choice tests ( $G$ -test for goodness-of-fit). The "no choice" column represents the number of parasitoids which made no choice of one of the odors.

females that emerged from *A. ludens* larvae reared on artificial diet ( $1.77 \pm 0.02$  mm) or grapefruits that were infested in the laboratory ( $1.77 \pm 0.02$  mm). Furthermore, the latter were significantly larger than parasitoids that developed from larvae reared in mango ( $1.65 \pm 0.02$  mm) ( $F = 14.54$ ;  $df = 4, 150$ ;  $P < 0.0001$ ) (Fig. 4). Parasitoids that developed in *A. ludens* larvae reared in mango were significantly larger than parasitoids that developed in *A. obliqua* reared in mango ( $1.53 \pm 0.03$  mm) ( $F = 10.79$ ;  $df = 1, 70$ ;  $P = 0.0016$ ) (Fig. 5). Longevity of parasitoid females emerged from *A. ludens* reared in grapefruits, both laboratory and wild Fp was significantly higher compared with parasitoids that developed from larvae reared in oranges. Parasitoid females from larvae reared in arti-

cial diet and mangos had the shortest lifetime ( $F = 13.67$ ;  $df = 4, 150$ ;  $P < 0.0001$ ) (Fig. 6). Parasitoids developing in *A. ludens* larvae reared in mangos had a significantly longer lifespan than when developing in *A. obliqua* larvae reared in mango ( $F = 10.22$ ;  $df = 1, 70$ ;  $P = 0.0022$ ) (Fig. 7).

**Parasitoid Fecundity.** The fecundity of *D. longicauda* females was highest when the parasitoid had developed in *A. ludens* larvae reared in mango. Females from fruit fly larvae reared in citrus were significantly less fecund. Fecundity was lowest when the female developed in a larvae reared in artificial diet ( $F = 5.79$ ;  $df = 4, 1,249$ ;  $P = 0.0001$ ). *A. ludens* larvae reared in mango produced more fecund female parasitoids than *A. obliqua* larvae from mango ( $F = 16.59$ ;  $df = 1, 716$ ;  $P = 0.0001$ ) (Table 2).

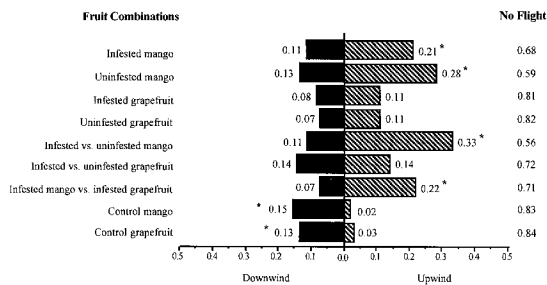


Fig. 3. Proportions of female parasitoids that flew upwind or downwind in the wind tunnel when exposed to different combinations of host fruits ( $n = 120$ , control  $n = 60$ ). Asterisks indicate significant differences within the choice tests ( $P = 0.05$ ) ( $G$ -test for the goodness-of-fit). The "no flight" column represents the proportion of parasitoids which showed no flight activity. The controls were citrus or mango trees without the respective fruits.

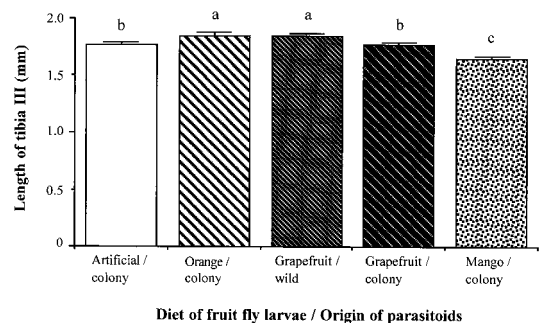
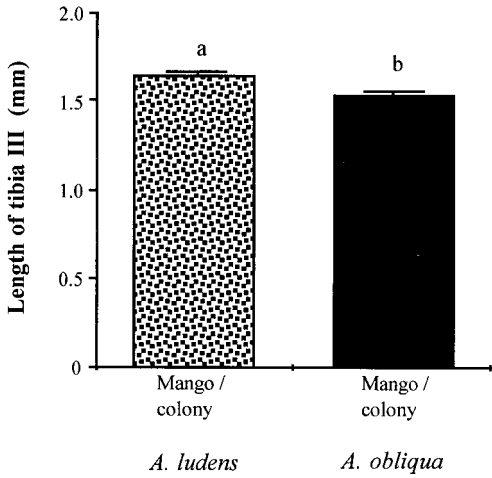


Fig. 4. Effect of the diet of *A. ludens* larvae on the size of female parasitoids (mean  $\pm$  SE). Parasitoid size is expressed as hind tibia length (mm). Data were analyzed by ANOVA, means were compared with an LSD test ( $P < 0.05$ ). Different letters indicate significant differences between means.





Diet of fruit fly larvae / Origin of parasitoids

Fig. 5. Effect of fruit fly species on the size of female parasitoids (mean  $\pm$  SE). Data were analyzed by ANOVA, means were compared with an LSD test ( $P < 0.05$ ). Different letters indicate significant differences between means.

**Sex Ratio of Progeny.** The diet of fruit fly larvae as well as the fly species had significant effects on the sex ratio of the progeny of *D. longicaudata* ( $F = 38.36$ ;  $df = 4, 1,249$ ;  $P < 0.0001$ ) (Table 2). Parasitoids emerged from *A. ludens* larvae reared in grapefruit (laboratory colony) had the highest proportion of female progeny, followed by orange and mango. *Anastrepha ludens* larvae reared in artificial diet produced parasitoid females with significantly lower numbers of female progeny. The lowest proportion of daughters was found in the progeny of parasitoids that developed from larvae reared in grapefruit, when the Fp generation was a wild cohort. No significant differences for the sex ratio of the parasitoid progeny was found when it developed in either fly species reared in mango ( $F = 0.82$ ;  $df = 1, 716$ ;  $P = 0.38$ )

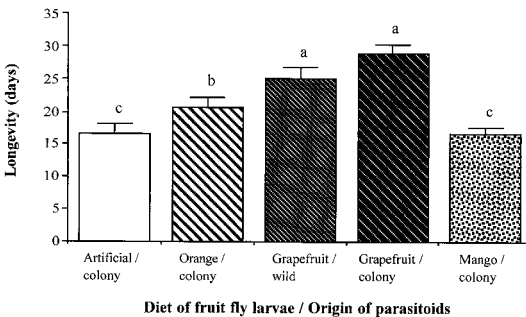
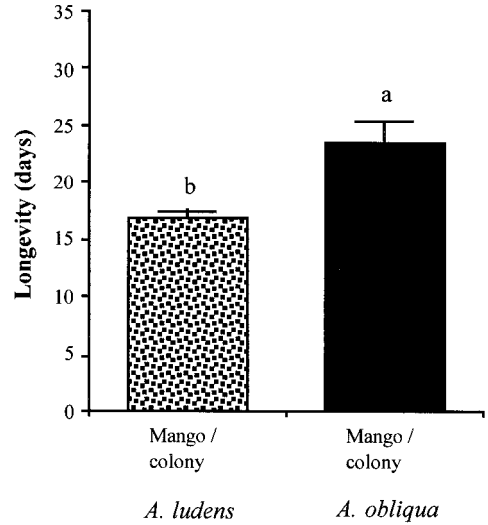


Fig. 6. Effect of the diet of *A. ludens* larvae on the longevity of female parasitoids (mean  $\pm$  SE). Data were analyzed by ANOVA, means were compared with an LSD test ( $P < 0.05$ ). Different letters indicate significant differences between means.



Diet of fruit fly larvae / Origin of parasitoids

Fig. 7. Effect of fruit fly species on the longevity of female parasitoids (mean  $\pm$  SE). Data were analyzed in an ANOVA, means were compared with an LSD test ( $P < 0.05$ ). Different letters indicate significant differences between means.

**Relationship Between Size and Longevity, Fecundity and Sex Ratio of Progeny.** Linear regressions (Sigmastat 1992) between parasitoid size and longevity, progeny number, and sex ratio of progeny did not detect any significant relationships.

## Discussion

We observed a significant effect of host fruits and fly species on preference and performance of parasitoid females. Parasitoids performed a higher number of flights in the wind tunnel in the presence of mangos.

Table 2. Proportion of parasitized fruit fly larvae (mean  $\pm$  SE) and sex ratios in the progeny of the F<sub>1</sub> generation of *D. longicaudata*

Diet of fly larvae/ Origin of parasitoids	Proportion of parasitized larvae	Sex ratio F <sub>2</sub> (males:total)
<i>Anastrepha ludens</i>		
Artificial/Colony	0.40 $\pm$ 0.020c	0.48bc
Orange/Colony	0.44 $\pm$ 0.016bc	0.34c
Grapefruit/Colony	0.45 $\pm$ 0.013b	0.24d
Grapefruit/Wild	0.45 $\pm$ 0.015bc	0.66a
Mango/Colony	0.52 $\pm$ 0.016aA	0.44bA
<i>Anastrepha obliqua</i>		
Mango/Colony	0.44 $\pm$ 0.011B	0.48A

Means within a column followed by different letters are significantly different at  $P < 0.05$ , LSD. a, different letters indicate significant differences between diets of *A. ludens*. A, different letters indicate significant differences between *A. ludens* and *A. obliqua* both reared on mango.

In the olfactometer, infested mangos and infested grapefruits were preferred over uninfested fruits. However, in choice tests, no significant preference for one of the fruits tested could be observed in the wind tunnel or the olfactometer. This, despite the fact that host fruit and fly host species significantly affected parasitoid size, longevity and reproductive success.

The attraction of naive parasitoids to fruit volatiles, observed in both host location experiments, indicate that *D. longicaudata* females appear to have an innate response toward olfactory cues. Our data support results of earlier studies (Nishida and Nampometh 1974, Greany et al. 1977, Messing and Wong 1992, Leyva et al. 1991). Contrary to the observations of Greany et al. (1977), in our assays *D. longicaudata* females responded strongly to fruit volatiles in a Y-tube olfactometer. Interestingly, parasitoids showed a clear preference for infested over uninfested fruit. This leads us to conclude that orientation toward the odor source occurred before and not after flight initiation as previously described by Greany et al. (1977). In the flight tunnel experiments we also observed that many females oriented toward the odor source clearly before flight initiation or walked along the floor of the tunnel toward the odor source. These observations seem to indicate that female parasitoids might be able to detect the infestation level of different fruit species from a short distance by using olfactory cues. To confirm this, field experiments on parasitoid foraging behavior are needed. Leyva et al. (1991) reported significantly stronger attraction of *D. longicaudata* females to grapefruit volatiles compared with mango volatiles in a wind tunnel experiment. But in contrast to our experiments, fruits were not offered in a choice situation. However, in our wind tunnel experiments we observed higher flight activity and stronger overall response of female parasitoids in the presence of volatiles and visual stimuli of mangos, regardless of their infestation level. These results provide support for the hypothesis that fruit volatiles are a major source of infochemicals that guide female parasitoids to the microhabitat of their hosts (Tumlinson et al. 1992). As already documented in earlier work done with the tephritid fly *Rhagoletis pomonella* (Walsh) (Aluja and Prokopy 1992, Aluja et al. 1993), presence of odor in the environment increased the level of activity of the tested insects. In our bioassays, parasitoids exhibited higher flight activity in the presence of fruits and trees when compared with those exposed to fruitless trees.

The significant effect of the 1st and 2nd trophic level over the 3rd, observed in our performance bioassay, clearly shows that host plant choice is important for the reproductive success of herbivores and their natural enemies. We observed significant differences in size, longevity, number, and sex ratio of parasitoid progeny for the host fruits and fly species tested. Although *A. ludens* larvae needed longer time to develop to 3rd instars when they fed in grapefruits compared with mangos and oranges (19 d in mango, 25 d

in oranges, 32 d in grapefruit, and 9 d in artificial diet, A.E., unpublished data), female parasitoids that developed from fly larvae fed in grapefruit lived significantly longer, were larger, and had higher proportions of female progeny. In a related study, Rodríguez (1991) reported that the proportion of females in the progeny was significantly higher in parasitoids developing in *A. obliqua* larvae reared in mango when compared with *A. ludens* larvae reared in oranges. We obtained contrasting results. In addition, our bioassay showed that those parasitoids that developed in *A. ludens* reared in mango had a higher proportion of female progeny than parasitoids that developed in *A. obliqua* from mango. In general, independent of fruit species, *A. ludens* was a better host for *D. longicaudata* females than *A. obliqua*. It is important to mention that in our study *A. ludens* larvae reared in artificial diet exhibited the fastest development rate, but produced female parasitoids with the shortest lifespan and the lowest fitness parameters. Parasitoids probably need nutrients that are only present in fruits. These aspects require further study and should be considered for mass rearing of parasitoids. The negative effects potentially exerted by the diet of fly larvae on the quality of mass reared and field released parasitoids might be of considerable importance for the success of biological control programs.

Our data do not support the hypothesis that an ovipositing female should prefer hosts that are best for its offspring (Rauscher 1985, Thompson 1988, Valladares and Lawton 1991). In this study, *D. longicaudata* females reacted more strongly to the odor of mangos, and parasitism rates were higher in *A. ludens* larvae reared in mango than in citrus. Despite this, the performance of their daughters was best when they developed in fruit fly larvae reared in grapefruit. Rodríguez (1991) also found under seminatural and laboratory conditions that a higher number of *D. longicaudata* females landed on mangos infested by *A. obliqua* and performed higher numbers of ovipositor probes than on oranges infested by *A. ludens*. However, parasitism rates in the respective fruits were not significantly different.

The genus *Anastrepha* is endemic to neotropical regions, but few of its native, noncommercial host plants are known with certainty (Aluja 1994). Both *Anastrepha* species used in our study are polyphagous (Aluja et al. 1987). *Anastrepha ludens* is mostly found in plants of the family Rutaceae, whereas *A. obliqua* infests mainly plants of the family Anacardiaceae (Hernandez-Ortiz and Aluja 1993). Grapefruit and mango, the host plants used in our preference and performance experiments, are exotic in Mexico. Citrus was introduced in 1518 (Ramírez 1979) and mango during the mid-1800s (Popenoe 1948). Despite this—on an evolutionary time scale—relatively recent introduction, both fly species have become economically important pests in cultivated mango and citrus species in Mexico. However, *A. ludens* performed better when developing in native *Casimiroa edulis* Llave and Lexington (Rutaceae) than in grapefruit (Diaz-Fleischer, personal communication), and *A. obliqua*

exhibited better measures of all demographic parameters after feeding in *Spondias mombin* L. (Anacardiaceae) than in mango (Toledo and Lara 1996). In Mexico, *S. mombin* is the preferred natural host plant of *A. obliqua* (Aluja and Liedo 1986). In the field, *A. obliqua* larvae are more frequently attacked by native parasitoids when feeding in *S. mombin* than in mango (Lopez et al. 1999). This observation might be an indication that the best food plant for the herbivorous insect also produces higher quality hosts for parasitoids (Mueller 1983, Benrey et al. 1998) and remains to be tested for this fruit fly—parasitoid system. *Dia-chasmimorpha longicaudata* is an exotic parasitoid that was first collected from *Bactrocera dorsalis* (Hendel) infesting mangos and guava in Southeast Asia (Bess et al. 1950, Clausen et al. 1965). It was introduced to Mexico for the control of *A. ludens* in 1954 (Wharton 1989). This parasitoid species is a generalist of various genera of fruit flies feeding on a number of different host plant families (Wharton et al. 1981). Under field conditions in Mexico, parasitism rates by this species were highest in *A. ludens* in *Citrus sinensis*, followed by *A. striata* in guava (*Psidium guava* L.), *Anastrepha* spp. in mango, and lowest in *A. obliqua* in *Spondias* sp. (Aluja et al. 1990). Lopez et al. (1999) reported *D. longicaudata* as the dominant parasitoid of *Anastrepha* in citrus, guava, and mango. In contrast, most of the *Anastrepha* pupae collected from *S. mombin* were parasitized by native parasitoids.

Our results correspond well with these data. *D. longicaudata* did not perform as well in *A. obliqua* larvae than in *A. ludens* larvae. This is a logical result given the fact that this association is rare under natural conditions (Lopez et al. 1999). In our study, we recorded the best performance of *D. longicaudata* in *A. ludens* larvae infesting the exotic hosts, grapefruit, and mango. Both are fruits from which it was originally collected in Asia. It thus appears that this parasitoid species is still not sufficiently well adapted to be able to successfully exploit the niche provided by native fruit fly species when infesting native host plants.

### Acknowledgments

We thank Daniel Sayago, Gabriela Jiménez, Antonio García, Guadalupe Trujillo, Gloria Lagunes, and Isabel Jácome for assistance during laboratory and field work. Mike Klungness (University of Hawaii) provided helpful comments on the design of the wind tunnel assay. This work was supported by grants from the Campaña Nacional contra las Moscas de la Fruta (SAGAR-IICA), U.S. Department of Agriculture, Office of International Cooperation and Development (OICD) (Project No. 198-23), USDA (No. 58-6615-3-025), Consejo Nacional de Ciencia y Tecnología - Sistema Regional del Golfo de México (No. 96-01-003-V), and a Postdoctoral Fellowship from the Institute of Ecology, UNAM, to A.E.

### References Cited

- Aluja, M. 1994. Bionomics and management of *Anastrepha*. *Annu. Rev. Entomol.* 39: 155–178.
- Aluja, M., and P. Liedo. 1986. Future perspectives on integrated management of fruit flies in Mexico, pp. 12–48. In M. Mangel, R. Plant and J. Carey [eds.], *Pest control: operations and systems analysis in fruit fly management*. Springer, New York.
- Aluja, M., and R. J. Prokopy. 1992. Host search behavior by *Rhagoletis pomonella* flies: intertree movement patterns in response to wind-borne fruit volatiles under field conditions. *Physiol. Entomol.* 17: 1–8.
- Aluja, M., J. Guillen, G. de la Rosa, M. Cabrera, H. Celedonio, P. Liedo, and D. H. Hendrichs. 1987. Natural host plant survey of the economically important fruit flies (Diptera: Tephritidae) of Chiapas, Mexico. *Fla. Entomol.* 70: 329–338.
- Aluja, M., J. Guillen, P. Liedo, M. Cabrera, E. Rios, G. de la Rosa, H. Celedonio, and D. Mota. 1990. Fruit infesting Tephritids (Diptera: Tephritidae) and associated parasitoids in Chiapas, Mexico. *Entomophaga* 35: 39–48.
- Aluja, M., R. J. Prokopy, J. P. Buonaccorsi, and R. T. Cardé. 1993. Wind tunnel assays of olfactory responses of female *Rhagoletis pomonella* flies to apple volatiles: effect of wind speed and odour release rate. *Entomol. Exp. Appl.* 68: 99–108.
- Barbosa, P., J. A. Saunders, J. Kemper, R. Trumbule, J. Olechno, and P. Martinat. 1986. Plant allelochemicals and insect parasitoids. Effects of nicotine on *Cotesia congregata* (Say) (Hymenoptera: Braconidae) and *Hyposoter annulipes* (Cresson) (Hymenoptera: Ichneumonidae). *J. Chem. Ecol.* 12: 1319–1328.
- Benrey, B., A. Gallejas, L. Rios, K. Oyama, and R. F. Denno. 1998. The effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. *Biol. Control* 11: 130–140.
- Bess, H. A., R. van den Bosch, and F. H. Haramoto. 1950. Progress and success of two recently introduced parasites of the oriental fruit fly, *Dacus dorsalis* Hendel, in Hawaii. *Proc. Hawaii. Entomol. Soc.* 14: 29–33.
- Clausen, C. P., D. W. Clancy, and Q. C. Chock. 1965. Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. *Agric. Res. Ser.* U.S. Dep. Agric. Tech. Bull. 1322.
- Dicke, M., and M. W. Sabelis. 1988. How plants obtain predatory mites as bodyguards. *Neth. J. Zool.* 38: 148–165.
- Elzen, G. W., H. J. Williams, and S. B. Vinson. 1986. Wind tunnel flight responses by hymenopterous parasitoid *Campoletis sonorensis* to cotton cultivars and lines. *Entomol. Exp. Appl.* 42: 285–289.
- Greany, P. D., J. H. Tumlinson, D. L. Chambers, and G. M. Boush. 1977. Chemically mediated host finding by *Biosteres (Opus) longicaudatus*, a parasitoid of tephritid fruit fly larvae. *J. Chem. Ecol.* 3: 189–195.
- Hedlund, K., L.E.M. Vet, and M. Dicke. 1996. Generalist and specialist parasitoid strategies of using odours of adult drosophilid flies when searching for larval hosts. *OIKOS* 77: 390–398.
- Hernandez-Ortiz, V., and M. Aluja. 1993. Listado de especies del género neotropical *Anastrepha* (Diptera: Tephritidae) con notas sobre su distribución y plantas hospederas. *Folia Entomol. Mex.* 88: 89–105.
- Lawrence, P. O. 1981. Host vibration—a cue to host location by the parasite, *Biosteres longicaudatus*. *Oecologia (Berl.)* 48: 249–251.
- Lawrence, P.O., P. D. Greany, J. L. Nation, and R. M. Baranowski. 1978. Oviposition behavior of *Biosteres longicaudatus*, a parasite of the caribbean fruit fly, *Anastrepha suspensa*. *Ann. Entomol. Soc. Am.* 71: 253–256.

- Leyva, J. L., H. W. Browning, and F. E. Gilstrap. 1991. Effect of hostfruit species, size, and color on parasitization of *Anastrepha ludens* (Diptera: Tephritidae) by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae). *Environ. Entomol.* 20: 1470-1474.
- Lopez, M., M. Aluja, and J. Sivinski. 1999. Hymenopterous larval-pupal and pupal parasitoids of *Anastrepha* species (Diptera: Tephritidae) in Mexico. *Biol. Control* 15: 119-129.
- Mattiacci, L., M. Dicke, and M. A. Posthumus. 1994. Induction of parasitoid attracting synomone in brussels sprouts plants by feeding of *Pieris brassicae* larvae: role of mechanical damage and herbivore elicitor. *J. Chem. Ecol.* 20: 2229-2247.
- Messing, R. H., and T.T.Y. Wong. 1992. An effective trapping method for field studies of Opiine braconid parasitoids of tephritid fruit flies. *Entomophaga* 37: 391-396.
- Messing, R. H., L. M. Klungness, E. B. Jang, and K. A. Nishijima. 1996. Response of the melon fly parasitoid *Psystalia fletcheri* (Hymenoptera: Braconidae) to host-habitat stimuli. *J. Insect Behav.* 9: 933-945.
- Mueller, T. F. 1983. The effect of plants on the host relations of a specialist parasitoid of *Heliothis* larvae. *Entomol. Exp. Appl.* 34: 78-84.
- Nadel, H., and J.J.M. van Alphen. 1987. The role of host- and host-plant odours in the attraction of a parasitoid, *Epidinocarsis lopezi*, to the habitat of its host, the cassava mealybug, *Phenacoccus manihoti*. *Entomol. Exp. Appl.* 45: 181-186.
- Ngi-Song, A. J., W. A. Overholt, P.G.N. Njagi, M. Dicke, J. N. Ayertey, and W. Lande. 1996. Volatile infochemicals used in host and host habitat location by *Cotesia flavipes* Cameron and *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae), larval parasitoids of stemborers on gramineae. *J. Chem. Ecol.* 22: 307-323.
- Nishida, T., and B. Napompeth. 1974. Trap for tephritid fruit fly parasites. *Entomophaga* 19: 349-351.
- Popenoe, W. 1948. Manual of tropical and subtropical fruits. Hafner, New York.
- Ramírez, J. M. 1979. Memoria del seminario de citricultura, pp. 23-35. In *La citricultura en México, problemas y perspectivas*. Fira, Monterrey, N.L., Mexico.
- Rausher, M. D. 1985. Variability for host preference in insect populations: mechanistic and evolutionary models. *J. Insect Physiol.* 31: 873-889.
- Rodríguez, R. 1991. Parasitismo y preferencia de *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) en tres especies de *Anastrepha* Schiner (Diptera: Tephritidae). Tesis de Maestría, Colegio de Postgraduados, Montecillo, Mexico.
- Sabelis, M. W., and H. E. Van de Baan. 1983. Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomol. Exp. Appl.* 33: 303-314.
- Sigmastat. 1992. Sigmastat, version 2.0 for Windows. Jandel, San Rafael, CA.
- Singer, M. C., D. Ng, and C. D. Thomas. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* 42: 977-985.
- Sivinski, J. 1991. The influence of host fruit morphology on parasitization rates in the caribbean fruit fly, *Anastrepha suspensa*. *Entomophaga* 36: 447-454.
- Sivinski, J., C. O. Calkins, R. Baranowski, D. Harris, J. Brambila, J. Díaz, R. E. Burns, T. Holler, and G. Dodson. 1996. Suppression of a caribbean fruit fly (*Anastrepha suspensa* (Loew), Diptera: Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biol. Control* 6: 177-185.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Freeman, New York.
- Statgraphics. 1991. Statgraphics, version 5.0. STSC. Statgraphics, Rockville, MD.
- Steinberg, S., M. Dicke, L.E.M. Vet, and R. Wanningen. 1992. Response of the braconid parasitoid *Cotesia* (= *Apanteles*) *glomerata* to volatile infochemicals: effects of bioassay set-up, parasitoid age and experience and barometric flux. *Entomol. Exp. Appl.* 63: 163-175.
- Thompson, J. N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomol. Exp. Appl.* 47: 3-14.
- Toledo, J., and J. R. Lara. 1996. Comparison of the biology of *Anastrepha obliqua* reared in mango (*Mangifera indica* L.) and in mombin (*Spondias mombin* L.) infested under field conditions, pp. 359-362. In B. A. McPherson and G. J. Steck [eds.], *Fruit fly pests. A world assessment of their biology and management*. St. Lucie Press, Delray Beach, FL.
- Tumlinson, J. H., T.C.J. Turlings, and W. J. Lewis. 1992. The semiochemical complexes that mediate insect parasitoid foraging. *Agric. Zool. Rev.* 5: 221-251.
- Turlings, T.C.J., J. H. Tumlinson, W. J. Lewis, and L.E.M. Vet. 1989. Beneficial arthropod behavior mediated by airborne semiochemicals. VIII Learning of host related odors induced by a brief contact experience with host by-products in *Cotesia marginiventris* (Cresson), a generalist larval parasitoid. *J. Insect Behav.* 2: 217-225.
- Valladares, G., and J. H. Lawton. 1991. Host-plant selection in the holly leaf-miner: does mother know best? *J. Anim. Ecol.* 60: 227-240.
- Vargas, R. I., J. D. Stark, R. J. Prokopy, and T. A. Green. 1991. Response of oriental fruit fly (Diptera: Tephritidae) and associated parasitoids (Hymenoptera: Braconidae) to different-color spheres. *J. Econ. Entomol.* 84: 1503-1507.
- Vet, L.E.M., and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37: 141-172.
- Vet, L.E.M., M. B. Sokolowski, D. E. MacDonald, and H. Snellen. 1993. Responses of a generalist and a specialist parasitoid (Hymenoptera: Eucilidae) to drosophilid larval kairomones. *J. Insect Behav.* 6: 615-624.
- Wharton, R. A. 1989. Classical biological control of fruit-infesting Tephritidae, pp. 303-313. In A. S. Robinson and G. Hooper [eds.], *World crop pests. Fruit Flies: their biology, natural enemies and control*, vol. 3B. Elsevier, Amsterdam, The Netherlands.
- Wharton, R. A., F. E. Gilstrap, R. H. Rhode, M. Fischel, and W. G. Hart. 1981. Hymenopterous egg-pupal and larval-pupal parasitoids of *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae) in Costa Rica. *Entomophaga* 26: 285-290.

Received for publication 24 November 1998; accepted 23 August 1999.